Novel Reconstruction of the Orientation of the Pectoral Girdle in Sauropods

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ABSTRACT

The orientation of the scapulocoracoid in sauropod dinosaurs is reconstructed based on comparative anatomical investigations of pectoral girdles of extant amniotes. In the reconstruction proposed here, the scapula of sauropods stands at an angle of at least 55° to the horizontal plane in mechanical coherence with the sternal apparatus including the coracoids. The coracoids are oriented cranioventrally to the rib cage and the glenoid is directed mediolaterally, which allows the humerus to swing in a sagittal plane. The inclination of the scapula to the horizontal plane is reconstructed for *Diplodocus* (60–65°), *Camarasaurus* (60–65°), and *Opisthocoelicaudia* (55–65°). The inclination of the scapulocoracoid has consequences for the overall body posture in *Camarasaurus* and *Opisthocoelicaudia*, where the dorsal contour would have ventrally declined toward the sacrum. Scapulocoracoid mobility depends on the arrangement of clavicles, the reconstruction of a coracosternal joint, and the reconstructed musculature of the shoulder girdle. In a crocodylian model of the shoulder musculature, m. serratus profundus and superficialis form a muscular sling, which suspends the trunk from the shoulder girdle and would allow a certain mobility of the scapulocoracoid. An avian model of the shoulder musculature would also mean suspension by means of the m. serratus complex, but indicates a closer connection of the scapula to the dorsal ribs, which would lead to more restricted movements of the scapulocoracoid in sauropods. Anat Rec, 290: 32–47, 2007.

Key words: sauropod; scapulocoracoid; sternal plate; pectoral girdle; mobility; functional morphology

Sauropod remains are mostly preserved with displaced shoulder girdles, so that their orientation in vivo cannot be directly concluded from taphonomy. Consequently, the reconstructed inclination of the scapulocoracoid toward the horizontal plane ranges between 10° and 60° (e.g., Hatcher, 1901; Osborn and Mook, 1921; McIntosh et al., 1997; Wilson and Sereno, 1998; Paul, 2000; Bonnan et al., 2005). The position of the scapulocoracoid in sauropods was discussed in the early 20th century in context with a debate on the overall posture of *Diplodocus*. Whereas scientists as Tornier (1909) and Hay (1908; 1910) argued for a "reptile-like" sprawling posture of the limbs of *Diplodocus*, which would have included a vertically positioned scapulocoracoid, Holland (1910) and Matthew (1910) favored a skeletal reconstruction of *Diplodocus* with vertical limbs, which was connected with a subhorizontally positioned scapulocoracoid. The latter two authors were then supported by Gilmore (1925), who in his description of an articulated skeleton of a juvenile *Camarasaurus* lentus stated that the right scapula of the specimen "was found in place" and therefore represents the in vivo position of the scapula in sauropods (Gilmore, 1925: p. 383) with an angle of ca. 45° to the horizontal plane (Fig. 1A and B). Such a position

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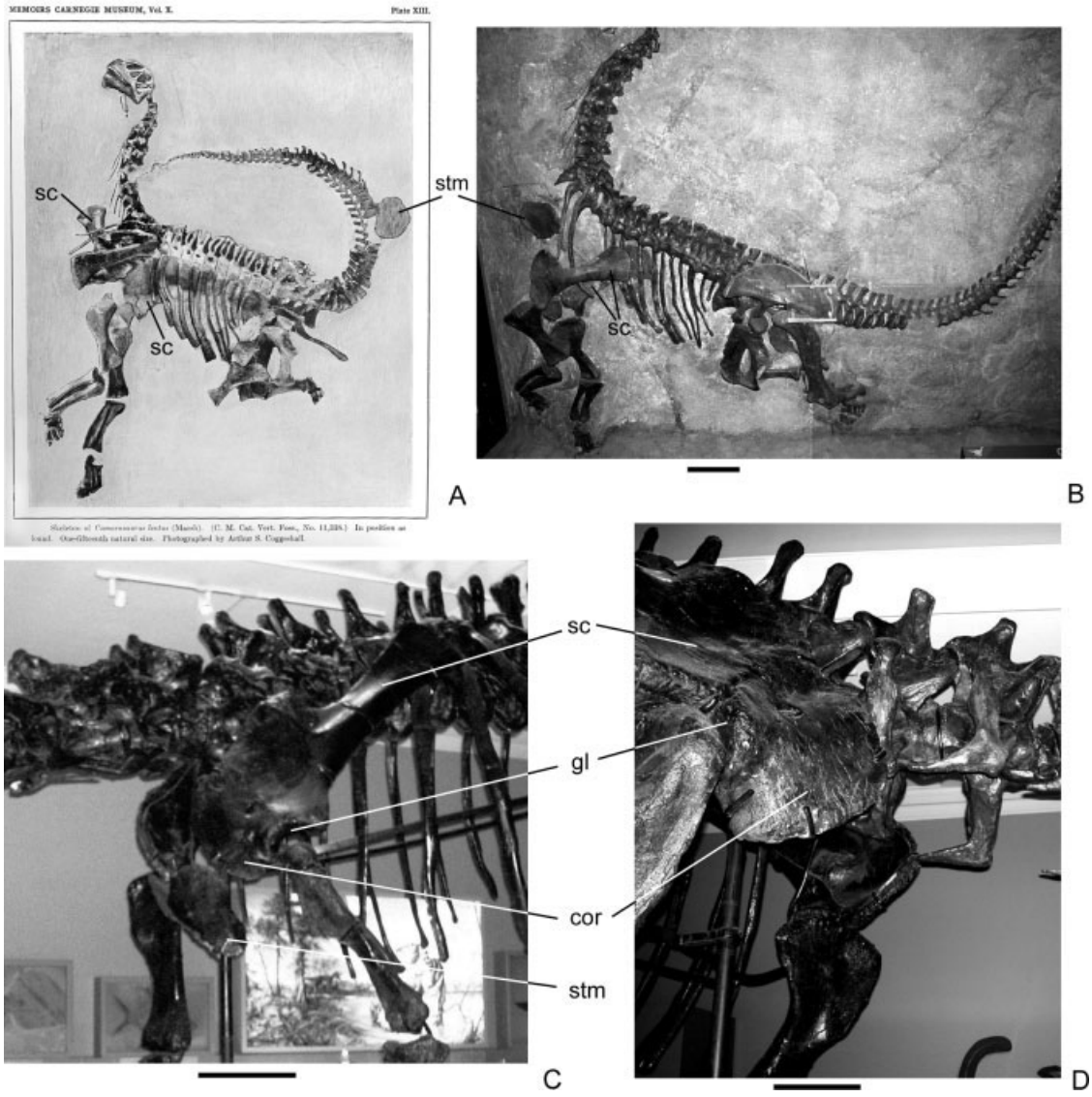

Fig. 1. Copy of photograph of articulated skeleton of *Camarasaurus lentus* (CM 11338): (**A**) in original position (from Gilmore, 1925) and (**B**) the rearranged skeleton of CM 11338 as on display in the Carnegie Museum in Pittsburgh. Position of the sauropod scapulocoracoid at the mounted skeletons of (**C**) *Diplodocus carnegii* (CM no. 84, 94 and 307) and (**D**) *Apatosaurus louisae* (CM no. 3018 and 11162) in the exhibitions of the Carnegie Museum in Pittsburgh. Scale bar = 10 cm. cor, coracoid; gl, glenoid; sc, scapula; stm, sternum.

of the scapula of 45° or less to the horizontal plane is consistent with the assumption that the glenoid notch must face straight ventrally to guarantee a graviportal forelimb configuration during stance and gait, and therefore is generally accepted until today (e.g., McIntosh et al., 1997; Wilson and Sereno, 1998; Upchurch et al., 2004).

In contrast to the rearranged specimen on display (CM 11338), an original photograph in Gilmore's paper (1925: Plate XIII) shows the specimen in situ with several limb bones displaced (Fig. 1A and B). For example, the left femur overlies the left scapula, which has rotated 180° so that its ventral portion is now facing dorsally. This suggests that the carcass was subject to disarticulation by drift prior to burial. Therefore, it cannot be excluded that the right scapula of the specimen also has been moved postmortem. It thus appears at least doubtful that the right scapula of CM 11338 is preserved in an in vivo position, rendering the topography of the sauropod pectoral girdle unresolved.

If the scapulocoracoidal apparatus of sauropods is oriented at varying angles of 45° or less to the horizontal plane, the coracoids often stand almost vertically in front of the cranial thoracic aperture (Fig. 1C and D). The connection between coracoids and sternal plates could be through bone-by-bone contact, which would be indicated by the presence of distinct contact areas at the coracoid and the sternal plates. The connection could also be synchondrotically, i.e., if coracoid and sternal plates would be embedded into a cartilaginous frame, which would for example be indicated by the presence of thickened and roughened bone margins being connected

with the cartilage. The vertically oriented coracoids in many sauropods may result in angled sternal plates, or in case of a synchondrotical contact, in an angled sternal cartilage, as was implied in several reconstructions (e.g., Borsuk-Bialynicka, 1977; McIntosh et al., 1997). Alternatively, to maintain the contact to the coracoids, the sternal plates can also stand more or less vertically in front of the rib cage (see for example reconstructional drawing of *Brachiosaurus* in Wilson and Sereno, 1998), which prevents their contact with the cranialmost sternal rib segments. In the latter case, the ventral wall of the bony rib cage would be completely free of bony reinforcement from the sternal apparatus.

Configurations of the elements of the pectoral girdle as described above are unknown in the sternal apparatus of extant amniotes with scapula and coracoid and emphasize the uncertainties about a proper arrangement of the pectoral girdle in sauropods. Because there is no evidence that the arrangement of the pectoral girdle in sauropods should differ from that of other terrestrial tetrapods with scapula and coracoid, general criteria on the arrangement of the pectoral girdle of extant amniotes (except Chelonia) should be applied. This results in a novel reconstruction of the arrangement of the pectoral girdle and its shoulder musculature as well as its consequences on muscular body suspension in the shoulder region for sauropod dinosaurs.

MATERIALS AND METHODS

For comparative anatomy, the following mounted skeletons of amniotes with scapula and coracoid were examined: *Caiman crocodylus* (SMNK), *Tomistoma schlegeli* (NMB, no collection number), *Varanus exanthematicus* (NMB no. C. 2139), *Ctenosaura acanthinura* (NMB no. 2719), *Chamaeleo vulgaris* (NMB no. 1636), *Sarcorhamphus gryphus* (NMB no. 3295), *Struthio camelus* (NMB no. 8180), *Dromaeus novahollandiae* (NMB no. 2978), and *Tachyglossus aculeatus* (NMB no. 6117). Although extant Chelonia do also possess a scapula and a coracoid, they were left out from these comparisons due to their special shell construction. Dissections were made of the shoulder girdle region of *Palaeosuchus palpebrosus* and *Columba livia* (private collection DS). Sauropod material, especially scapulocoracoids and sternal plates, were examined in the following collections: American Museum of Natural History (AMNH), New York, New York; Carnegie Museum of Natural History (CMNH), Pittsburgh, Pennsylvania; Chengdu University of Technology (CDUT), Chengdu, China; Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Beijing, China; Museum für Naturkunde, Berlin (MNB), Germany; Naturhistorisches Museum Basel (NMB), Basel, Switzerland; Saurier-Museum Aathal (SMA), Switzerland; Naturmuseum Senckenberg (NMS), Frankfurt, Germany; National Museum of Natural History, Smithsonian Institution (NMHNSI), Washington, District of Columbia; and Yale Peabody Museum (YPM), New Haven, Connecticut.

Commonly, a phylogenetically grounded approach is chosen for the interpretation of soft tissue, osteological, and functional morphological data from extant and extinct taxa using the Extant Phylogenetic Bracket (EPB) (Witmer, 1995, 1997; but see also for an example Carrano and Hutchinson, 2002). In the case of this work, the EPB helps to determine the possibilities and limits within which aspects of the sauropod shoulder girdle can be deduced. A robust phylogenetic tree exists for sauropods, placing them into Saurischia, bracketed by the two extant outgroups Crocodylia and Aves (see for example Witmer, 1997). Within Saurischia, their closest fossil outgroups are prosauropods and theropod dinosaurs (see for example Upchurch et al., 2004). These outgroups have to be included into discussion for a better understanding of the historical context and limits of the evolution of the shoulder girdle in sauropods.

However, EPB does not work without problems here. The pectoral girdle of birds is strongly adapted to flight (Dial et al., 1991); that of quadruped crocodylians is adapted to an amphibious mode of life (Meers, 2003). Both Aves and Crocodylia are therefore highly derived bracket members that give only limited information to a functional model of the sauropod pectoral girdle. Sauropods themselves represent a special body construction, in particular concerning their gigantic body size and the columnar, vertically held limbs. For a functional morphological study, it is therefore useful to apply also analogous functional suites based on the principles of biomechanics and comparative anatomy. Thus, all extant amniotes where scapulae and coracoids show a similar shape to those of sauropods were included into the reconstruction of a possible arrangement of the pectoral girdle in sauropods. In the end, while a phylogenetically grounded approach helps to draw conclusions on evolutionary similarities and the development of morphological novelties, an analogous functional approach reveals constructional similarities to explain similar functional suites in different groups of animals. The combination of both approaches, which has been applied already to other aspects of tetrapod biology (Perry and Sander, 2004), supports here a plausible model for both the anatomy and functional morphology of the sauropod shoulder girdle.

The shape of a bone reflects how it was loaded primarily during life (Wolff, 1892; Koch, 1917; Witzel and Preuschoft, 2005). Therefore, the reconstruction of the orientation and distribution of the muscles and tendons inserting at a bone of an extinct animal must provide a consistent functional morphological model in the context of an assumed main loading force that acts on the bone. This force can be displayed either as a vector along the line of action of a certain muscle or as the resultant of two forces in a force parallelogram composed by the vector of a certain muscle and the vector representing weight or inertia. The depicted vectors are the result of the reconstruction of tendinomuscular systems as obtained by soft tissue reconstructions following EPB. Only the topographical distribution of the muscles can be reconstructed here, with their pulling directions reconstructed according to the directions of inserting tendons, the aponeuroses of assumed fiber direction.

For the reconstruction of the arrangement of the sauropod shoulder region, the arrangement of the shoulder regions of those extant amniotes was used, where scapulae and coracoids show a similar shape to those of sauropods, thus applying an actualistic aspect of comparative anatomy. Despite the differences in the absolute body mass of the extant analogues and possible differences in physiology, the similarly shaped bones indicate a similar load implied by the resultants of the body weight or inertial forces and muscle force during locomotion and

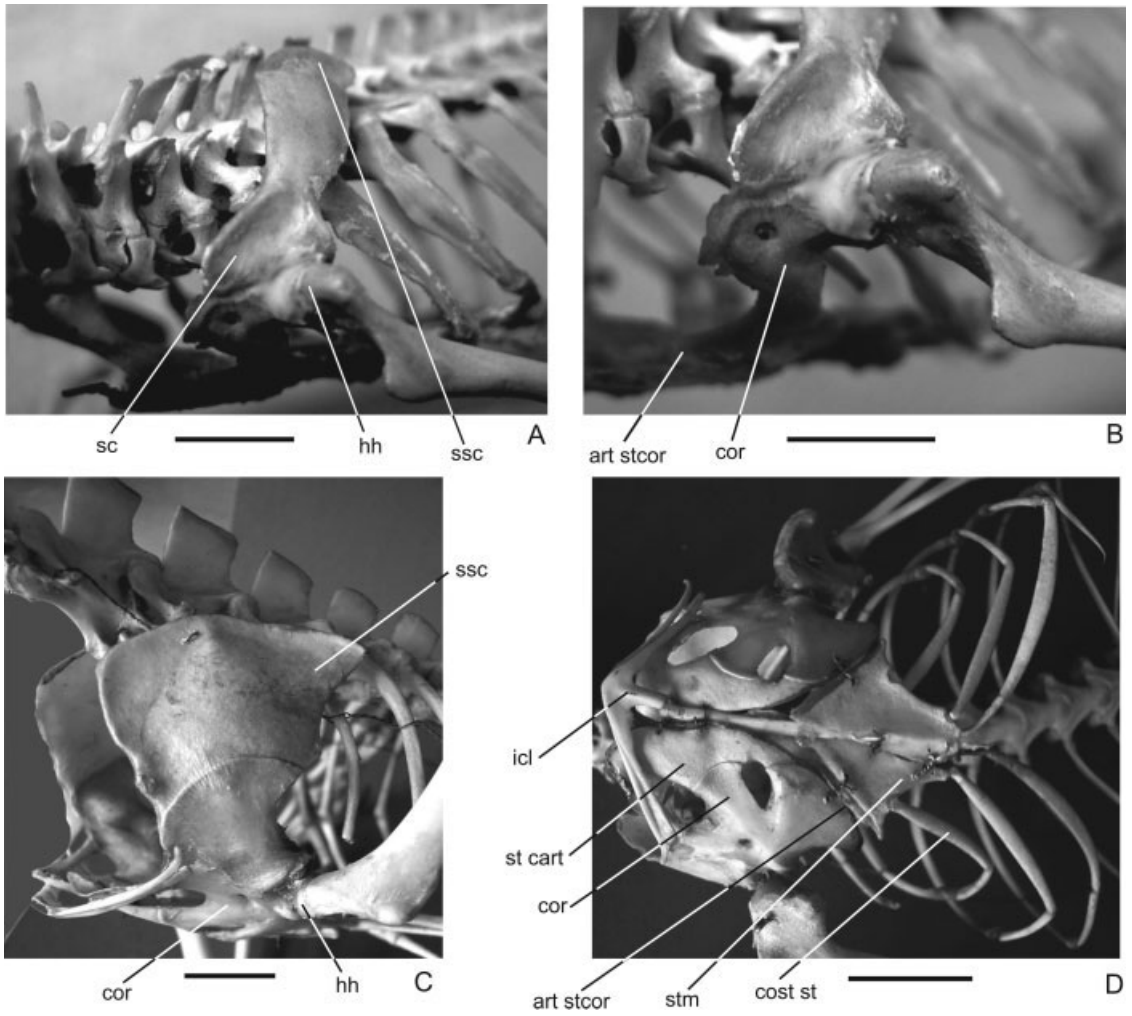

Fig. 2. Photographs of mounted skeletons of extant Crocodylia and Lepidosauria showing the position of scapula and coracoid in extant amniotes. Pectoral girdle of *Caiman crocodylus* (SMNK): (**A**) in left lateral view and (**B**) closeup of craniolateral view showing the medially directed coracoid. Pectoral girdle of *Varanus exanthematicus* (NMB no. C. 2139): (**C**) in left craniolateral view and (**D**) in ventral view. Scale bar = 5 cm. art stcor, sternocoracoidal articulation; cor, coracoid; cost st, sternal rib; hh, humerus head; icl, interclavicula; sc, scapula; ssc, suprascapula; stm, sternum.

thus a similar biomechanical behavior (cf. Salisbury, 2001).

RESULTS

Position and Orientation of Pectoral Girdle in Extant Amniotes

In extant crocodylians, the scapula overlies parts of the lateral surface of the eighth cervical to second thoracic ribs (Fig. 2A). The long axis of the scapular blade is caudally inclined at an angle of about 50° to the horizontal plane. A cartilaginous suprascapula is attached to the broadened and craniocaudally extended dorsal margin of the scapula and is medially inclined from the latter. The coracoid is as long as the scapula. The long axis of the coracoid is curved, so that the coracoid is directed from the glenoid fossa ventromedially to the cartilaginous sternum (Fig. 2B). A longitudinally oriented, median, rod-like interclavicula is enclosed into the cartilaginous sternum (Meers, 2003) and reaches caudally between the medial margins of the coracoideal wings. The sternal apparatus forms the ventral wall of the thoracic cavity. The medial ends of the cranialmost eight cartilaginous sternal rib segments articulate with its lateral margin. Cranially, the sternal plate is in contact with the ventromedial margins of the coracoids (Fig. 2B). Caudally, eight cartilaginous sternal and laterocostal elements connect the sternal apparatus with the first to eighth cranial thoracic ribs (Wettstein, 1937; Frey, 1988a). Cranial rotation of the scapulocoracoid complex of extant Crocodylia is reported by Meers (2003) to be achieved during protraction of the forelimb by means of m. trapezius and m. levator scapulae. Additionally, the coracosternal joint was found to be mobile, allowing the coracoid to be pulled caudally relative to the sternum, probably by means of m. costocoracoideus pars superficialis et profunda (Meers, 2003).

The morphology of scapula and coracoid varies considerably within extant lepidosaurs. Mostly, the bony part of the scapula extends only slightly dorsal to the glenoid

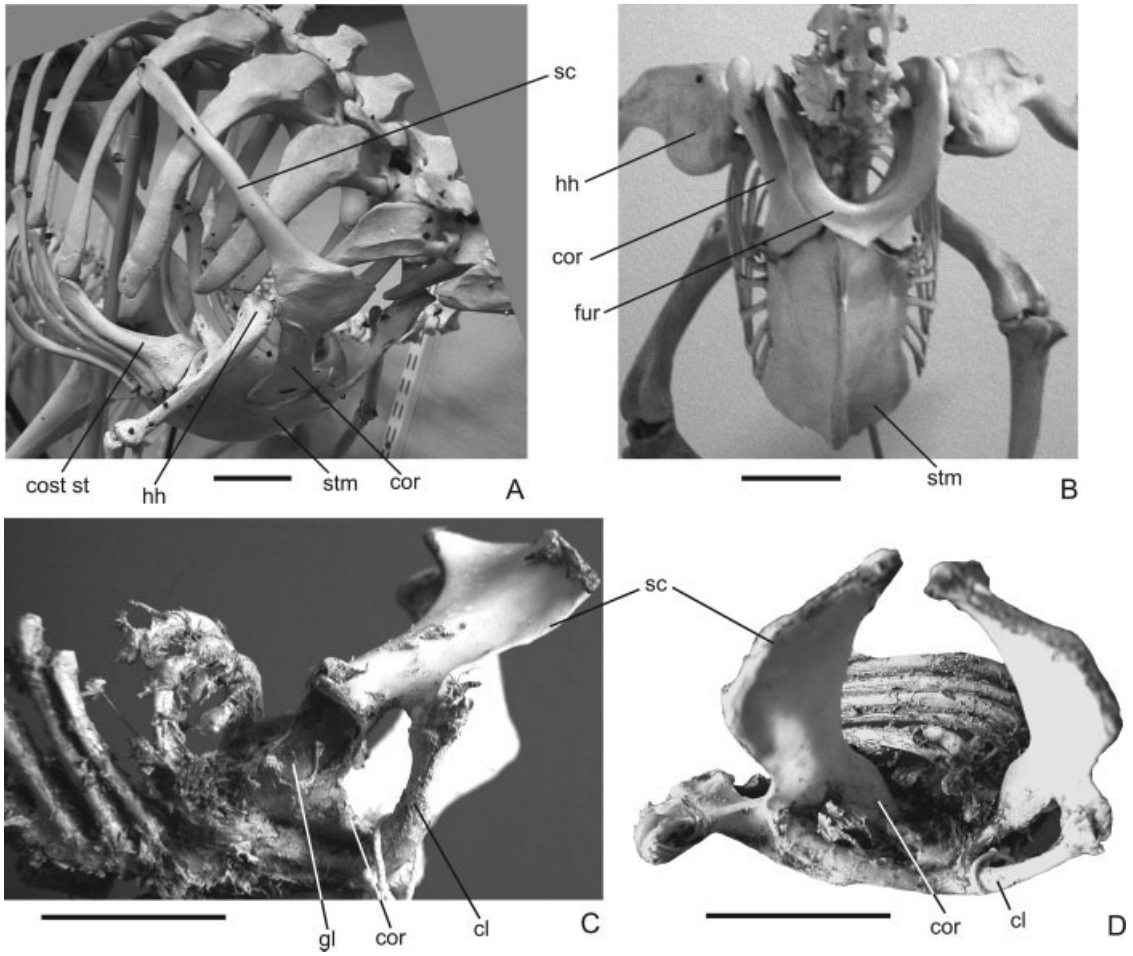

Fig. 3. Photographs of mounted skeletons of extant Aves and Monotremata showing the position of scapula and coracoid in extant amniotes. **A:** Right lateral view of pectoral girdle of *Dromaeus novahollandiae* (NMB no. 2978). **B:** Cranial view of pectoral girdle of *Sarcorhamphus gryphus* (NMB no. 3295). Isolated pectoral girdle with dorsal ribs of *Tachyglossus aculeatus* (NMB no. 6117): (**C**) in right lateral view and (**D**) in cranial view, with some dried muscle fibers and ligaments still in place. Scale bar = 5 cm. cl, clavicula; fur, furcula; gl, glenoid.

fossa (Fig. 2C). However, the bone diverges rapidly to a long dorsal margin that bears a large suprascapula (Starck, 1979; Jenkins and Goslow, 1983). The plate-like coracoid can be perforated and is often synostosed with the scapula. From the glenoid fossa, the coracoid curves ventromedially and, with its medial margin, contacts the horizontally oriented cartilaginous sternum (Fig. 2D). This coracosternal articulation can form a synovial joint, such as in *Varanus* (Jenkins and Goslow, 1983). In this case, a groove is developed at the lateral margin of the sternum, into which the cartilaginous coracoidal cartilage fits (Fig. 2D). The interlocking sternal and coracoidal cartilage at this joint allows only longitudinal sliding of the coracoid along this joint, whereas a separation of the sternum and coracoid is prevented. The longitudinal part of the median T-shaped interclavicula reaches between the medial margins of the coracoids and is firmly connected to the caudally adjacent sternum (Fig. 2D). The clavicles contact with their medial part the lateral processes of the interclavicula and with their lateral part articulate with the cranial margin of the scapula (Jenkins and Goslow, 1983). Thus, the clavicles connect the interclavicula with the cartilaginous sternal apparatus. As in crocodylians, the sternal apparatus forms the ventral wall of the thoracic cavity and laterally connects with the cartilaginous sternal rib segments of the first to fifth or sixth cranial thoracic ribs (Starck, 1979).

Extant birds are bipeds and their shoulder girdle is an integral element of the flight apparatus, which underwent fundamental evolutionary transformations. The scapula of birds is blade-like and aligned parallel to the thoracic vertebrae, covering the cranialmost five dorsal ribs (Fig. 3A). The coracoids are shifted cranial to the rib cage, and they point caudoventrally from the glenoid fossa and articulate with the cranial margin of the large bony sternum (Baumel and Witmer, 1993). The furcula represents the fused clavicles and lies in front of the coracoids and rib cage (Fig. 3B). The furcula is laterally tightly connected to the dorsal ends of the coracoids and the cranial ends of the scapulae (Jenkins et al., 1988). Caudally to the coracosternal articulation, the bony sternal rib elements articulate with the dorsolateral margin of the trough-shaped sternum (Fig. 3A and B). As in lepidosaurs and crocodylians, the sternum forms the ventral wall of the thoracic cavity. The coracoids form struts to stabilize the shoulder frame against the power of the

flight muscles. During upstroke-downstroke transition and during downstroke, the coracoids are also caudolaterally translated along the coracosternal joint, which leads to lateral displacement of their dorsal ends (Jenkins et al., 1988). Similarly, a lateral spread of the dorsal ends of the furcula during downstroke leads to a medial displacement of the caudal ends of the scapulae (Jenkins et al., 1988; Goslow et al., 1989). Resulting from the orientation and position of the coracoids, the glenoid fossa lies in the same horizontal plane as the vertebral column.

Monotremes are the only mammals that possess bony coracoids (Starck, 1979; Kardong, 1998). These coracoids are plate-like and lie ventromedially adjacent to the scapula to contact the bony sternum and interclavicula (Fig. 3C). The claviculae attach cranially to the scapulae and contact each other in the median plane (Fig. 3D). The bony sternal rib elements of the cranialmost five thoracic ribs articulate to the sternum in the horizontal plane. Sternum and interclavicula are oriented parallel to the distal ends of the thoracic ribs and form the ventral wall of the thoracic cavity. The glenoid fossa lies level with the sternum in a horizontal plane (Fig. 3C and D).

The comparisons between crocodylians, lepidosaurs, birds, and monotremes as extant amniotes with coracoid and scapula do allow the following general conclusions concerning the arrangements of the elements of the pectoral girdle.

First, the bony and cartilaginous sternal elements form the floor of the thoracic cavity. Both elements together form a plate, to the lateral margins of which the sternal rib segments articulate. The orientation of the sternal plate depends on the ventral extension of the thoracic ribs. If the ribs terminate on a horizontal plane, the sternal plate is oriented horizontally as well, as in crocodylians, lepidosaurs, and monotremes. If the line of the distal termini of the thoracic ribs descends caudoventrally, the sternal plate is inclined in the same direction, as in modern birds. From this, it can be concluded that the sternal plate generally tends to parallel the line connecting the distal termini of the thoracic ribs. This helps to reconstruct the position and orientation of the sternal plates in amniotes whenever a sufficient number of thoracic ribs is preserved for the reconstruction of the line of their distal termini.

Second, the orientation of the coracoid with respect to the median plane of the body depends on the orientation of the articulation between the coracoid body and the sternal plate: the orientation of the coracoid must allow an articulation between the coracoid body and the sternal plate. If it is possible to reconstruct any part of the coracosternal articulation, the orientation of the coracoid can be determined with high reliability.

Third, the scapula always overlays the cranialmost thoracic ribs laterally. With the exception of extant birds, the long axis of the scapula is oriented close to the vertical.

Position and Orientation of Pectoral Girdle in Prosauropods

Scapula and coracoid are unfused in prosauropods (Huene, 1926; Galton, 1973, 1984; Cooper, 1981; Van Heerden and Galton, 1997). The scapula is slender and elongate, and its dorsal end is expanded and thickened. The plate-like coracoid is craniocaudally oval in outline (Huene, 1926; Galton, 1973; Cooper, 1981). The glenoid is a wide V-shaped notch that faces caudoventrally in case that the scapulocoracoid is aligned with an angle of ca. 45° to the line of the vertebral column (Cooper, 1981: *Massospondylus*; Galton, 2001: *Plateosaurus*). Claviculae are known from *Plateosaurus* and *Massospondylus* (Huene, 1926; Cooper, 1981; Galton, 2001; Yates and Vasconcelos, 2005). In *Massospondylus*, the claviculae are preserved in situ as structures laterally contacting the acromial region of the scapula and medially overlapping, forming a brace between the scapulae in front of the rib cage (Yates and Vasconcelos, 2005). A pair of sternal plates is known in prosauropods. Its shape varies from taxon to taxon from suboval to rounded and triangular (Huene, 1926; Cooper, 1981; Galton and Upchurch, 2004). The sternal plates were probably medially connected to each other by cartilage (Galton and Upchurch, 2004). The sternal plates bear a cranial coracoid articular facet that indicates its position caudally adjacent to the coracoids, joined to the latter by cartilage. At least some prosauropods seem to have been fully bipedal (e.g., *Plateosaurus*, *Massospondylus*) (Senter and Bonnan, 2005; Bonnan and Senter, 2007), whereas for others, only a facultative bipedal posture is assumed (Christian and Preuschoft, 1996; Galton and Upchurch, 2004).

Reconstructed Arrangement of Pectoral Girdle in Sauropods

The sauropod pectoral girdle consists of a pair of scapulae and coracoids (Fig. 1). The elements on either side are fused to a scapulocoracoid in adults (McIntosh, 1990). There are plate-like paired bony sternal plates and cartilaginous sternal elements (Filla and Redman, 1994; Claessens, 2004). The paired bony sternal plates in sauropods were embedded in a cartilaginous matrix, which is indicated by the rugosities on the margins of the bony sternal plates (Fig. 1C). Therefore, the presence of a combined bony-cartilaginous sternal plate in sauropods is likely, but its outline and caudal expansion cannot be reconstructed at present knowledge.

The expanded, rugose, ventral ends (termini) of the cranial dorsal ribs indicate the presence of cartilaginous sternal elements (Borsuk-Bialynicka, 1977). Several sauropod specimens are complete enough to reconstruct the line of the distal termini of the ribs. In all sauropods, the line across the termini of the ribs descended along the cranialmost five or six pairs of dorsal ribs. We therefore conclude that the sternal plate was inclined caudoventrally. The sternal plate must have been positioned at a short distance ventrally to the bony rib cage, allowing the contact to the cartilaginous sternal rib segments. According to the shape of the bony sternal plates, the whole bony-cartilaginous sternal plate was plane. As integral parts of the sternal apparatus, the coracoids should be connected with the sternal plates. The medial contact surfaces of the coracoids articulated with the cranial or lateral margin of the bony sternal plate. As a consequence, the coracoid must have been oriented cranioventral to the rib cage. Because scapula and coracoid were fused, this coracoid position brings the scapula into a position lateral to the cranialmost dorsal ribs with its blade standing at an angle of at least 55° to the line of the vertebral column.

Enough parameters are preserved to reconstruct arrangement and orientation of all shoulder and sternal elements in sauropods based on the criteria established on the basis of extant amniotes as described above. In order to demonstrate the consistency of this reconstruction method, the arrangements of the pectoral girdle of *Diplodocus*, *Camarasaurus*, and *Opisthocoelicaudia* as obtained from their osteology are described here.

***Diplodocus*.** In neutral position, when all intervertebral joints are in the middle position, the dorsal vertebrae of *Diplodocus* form a straight line (see Stevens and Parrish, 1999: Fig. 2B). Between the first and fifth dorsal vertebra, the dorsal ribs of *Diplodocus* increase in length, so that the line of the distal termini of the ribs descends caudoventrally between the first and fifth dorsal rib. The broadened and roughened ventral margin of the first to fifth dorsal rib indicates that these ribs continued into a cartilaginous sternal rib segment.

In *Diplodocus*, the scapular blade is slightly laterally convex (Hatcher, 1901; McIntosh, 1990) and the ventral half of the coracoid curves from the scapula ventromedially (Fig. 1C). The expanded dorsal end of the scapular blade and its rugose dorsal margin indicate that a cartilaginous suprascapula was present. The glenoid portion of the scapula is twice as long as that of the coracoid and, viewed from caudally, both are oriented at right angles to each other. The rough and uneven medial and caudal margins of the coracoids indicate a cartilaginous contact of them along the median line and mark caudally the contact with the sternal plates (Fig. 1C). The nature of this contact cannot be reconstructed with more detail, but it is possible that the median intercoracoidal contact and the sternocoracoidal contact were mobile to a certain degree. In *Diplodocus* carnegii, a pair of rounded triangular bony sternal plates is preserved (Hatcher, 1901; Holland, 1906; McIntosh, 1990; Upchurch et al., 2004). The cranial, caudal, and lateral margins of the sternal plates are rough, which indicates that they were surrounded by cartilage, forming a bony-cartilaginous plate lateral to which the sternal ribs are attached. The straight and thickened medial margin of the sternal plates indicates a cartilaginous contact between them along the median line. Rod-like clavicles with paddle-shaped medial ends are described by Hatcher (1901) for *Diplodocus*; however, their correct identification is still doubted (Upchurch et al., 2004). Because the morphology and length of the bones described and figured by Hatcher (1901: p 41) and Holland (1906: p 257–258) are consistent with that of the clavicula in extant lepidosaurs (Starck, 1979), and prosauropods such as *Massospondylus* and *Plateosaurus* (Yates and Vasconcelos, 2005), we consider these bones to be appropriately determined as claviculae.

If the sternal plates lay parallel to the caudoventrally inclined line of the ventral termini of the ribs, they were caudoventrally inclined too at more or less the same angle. The width of the trunk, as indicated by the lateral extension of the transverse processes and their articulated ribs, increased between the first and fourth dorsal vertebra. Therefore, it appears likely that the scapulae converged cranially. Assuming a cartilaginous contact between the cranial margins of the bony sternal plates and the caudal margins of the coracoids, the scapulocoracoid of *Diplodocus* in vivo must have been inclined ventrocranially at an angle of approximately 60–65° to the horizontal plane in lateral view (Fig. 4A and B). Only with such an inclination would the coracoids be continuous with the sternal plates (Fig. 4B and C). With this inclination, the scapula overlay the first to third dorsal ribs laterally. The scapular blade terminated dorsally level with the base of the neural spines of the dorsal vertebrae. The dorsal margin of the suprascapula could have lain at maximum level with the dorsal extremities of the neural spines and due to our reconstruction would have extended the height of the scapula by one-third (Fig. 4A and B). The narrow cranial width of the trunk would allow the coracoids to contact each other in the median plane directly cranially to the rib cage, which is consistent with the assumption of their cartilaginous median contact. Due to the curvature of the coracoid, the long axis of the glenoid fossa would have extended from cranioventrally to caudodorsally with the coracoidal part positioned medioventrally to the scapular part of the glenoid fossa. This orientation of the glenoid fossa would have allowed a vertical position of the humerus of *Diplodocus* directly lateroventral to the rib cage during stance (Fig. 4C).

Two alternative arrangements have to be discussed for the claviculae of *Diplodocus*. The claviculae could have lain cranially adjacent to the craniolateral part of the coracoid and the cranial part of the scapula (Fig. 4D), being medially close to each other but without direct median contact (Holland, 1906). This arrangement would represent a nonbracing model sensu Yates and Vasconcelos (2005). The position of the clavicles cranially contacting the rest of the shoulder girdle would also correspond to the condition found in lepidosaurs, such as *Varanus* (Jenkins and Goslow, 1983). In *Varanus*, this arrangement of the claviculae is combined with a synovial joint between coracoid and cartilaginous sternum responsible for longitudinal movements of the scapulocoracoid complex, whereas the clavicles do not contribute to such movements (Jenkins and Goslow, 1983). There is no evidence for such a coracosternal joint in *Diplodocus*, although this joint could have been purely cartilaginous. The nonbracing model of clavicula arrangement in *Diplodocus* could indicate two additional articulations (scapuloclavicular and coracoclavicular) in the pectoral girdle that could have a similar role as the lepidosaurian coracosternal joint. These articulations would enhance a slight craniocaudal tilting of the scapulocoracoid by contraction of m. serratus profundus/m. serratus superficialis, leading to a craniocaudal tilting of the scapular blade. This would lead also to a tilting of the glenoid notch and sliding movement of the sternal plates against each other. The humeral head in *Diplodocus* is two-thirds the width of the glenoid fossa, yielding a limited mobility of the humerus. Craniocaudal tilting of the scapulocoracoid would have resulted in an increasing range of motion of the humerus, but only during pro- and retraction (Bonnan, 2003). The arrangement of claviculae in *Diplodocus* in a nonbracing model might therefore indicate that stride length of the forelimb was increased by controlled tilting movements of the scapulocoracoids.

Alternatively, the claviculae of *Diplodocus* could have been arranged with their lateral part contacting the acromial region of the scapula and their medial flattened parts overlapping each other cranioventrally to the acro-

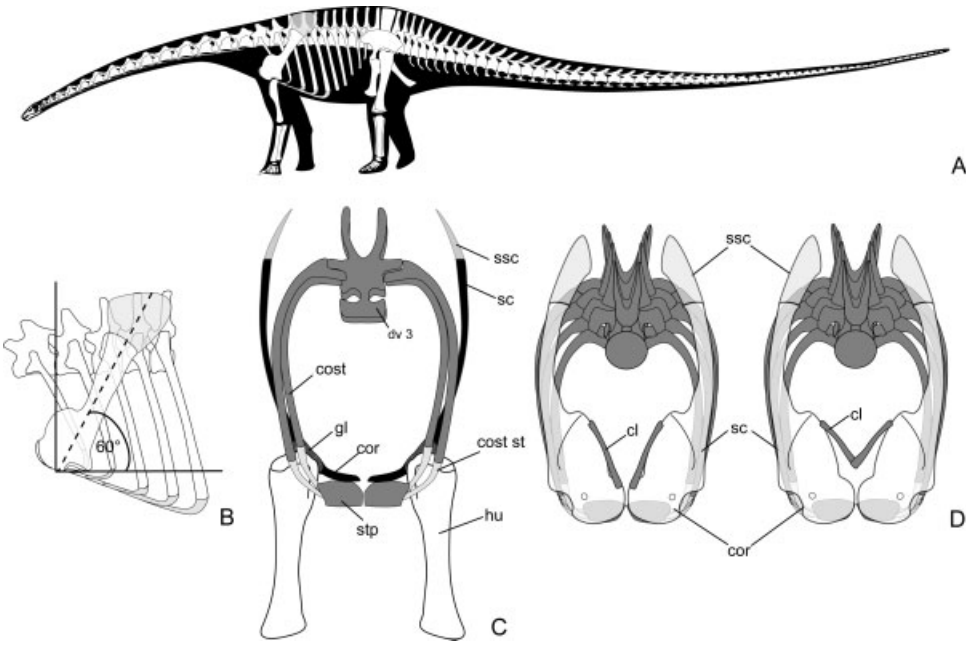

Fig. 4. Reconstruction of the pectoral girdle of *Diplodocus* on the basis of the skeleton of *Diplodocus carnegii* (CM 84 and 94). **A:** Reconstruction of the skeleton in left lateral view with an angulation of the scapula of 60° to the horizontal plane. **B:** Blowup of scapulocoracoid with cranial dorsal vertebrae and rib cage: the angulation of the scapulocoracoid to the horizontal plane is measured in lateral view along the long axis of the scapular blade. **C:** Oblique caudal view of the shoulder girdle at the level of the second and third dorsal vertebra showing position of the glenoid and curvature of the scapulocoracoid. **D:** Cranial view of the shoulder girdle with reconstruction of the position of the claviculae as nonbracing model (left) and with overlapping contact to each other in the middle (right). Not to scale. cost, dorsal rib; dv, dorsal vertebra; hu, humerus; stp, sternal plate.

mion (Fig. 4D). Thus, the claviculae would form a V-shaped arrangement, similar to the in situ preserved claviculae in the prosauropod *Massospondylus* (Yates and Vasconcelos, 2005). Because the claviculae of *Diplodocus* were not fused to each other, they would have needed to be medially fixed to each other by cartilage or fibers of connective tissue. This clavicular arrangement would have induced a reduction of the mobility of the scapulocoracoids of *Diplodocus* compared to the nonbracing model, but not as much as with the fused furcula of theropod dinosaurs (Makovicky and Currie, 1998) and birds (e.g., Jenkins et al., 1988). Apparently, completely fused claviculae or furculae are restricted to bipedal taxa. During quadruped locomotion, the part of the shoulder girdle connected to the loaded limb is tilted toward the unloaded body side by the vertical component of the ground reaction force and exposed to rotational loads directed opposite to the direction of propulsion (Jenkins, 1971; Jenkins and Goslow, 1983; Carrier, 1993), which would most probably lead to breakage of co-ossified claviculae in *Diplodocus*. Reduction of the mobility of the scapulocoracoids would be consistent with the presence of bird-like rib facets in sauropods (Bonnan et al., 2005).

With 65° a cranioventral inclination of the scapula, the scapulocoracoid in *Diplodocus* was more vertical in vivo than previously suggested (e.g., Hatcher, 1901, 1903; McIntosh et al., 1997). This reconstruction brings the shoulder girdle further dorsal with respect to the sacral region. Because the dorsal vertebrae form a straight line in articulation in the neutral pose (see reconstruction in Stevens and Parrish, 1999) and the dorsal neural spines get taller toward the sacrum, the dorsal contour of *Diplodocus* would have very slightly increased in height toward the sacrum, decreasing in cranial direction and caudal to the sacrum (Fig. 4A).

Camarasaurus. In neutral position, the dorsal vertebrae of *Camarasaurus* form a straight line. The dorsal ribs are directed caudoventrally in lateral view and their corpora are arched caudally (Fig. 1B). Those of the first through sixth dorsal ribs are one-third broader than those of the subsequent six pairs of ribs, ventrally expanded and rugose. The first to fifth dorsal ribs of *Camarasaurus* increase in length, so that the line of the distal termini of the ribs descends caudoventrally between the first and fifth rib.

The scapular blade of *Camarasaurus* is laterally weakly convex and expands cranioventrally into the acromial process (Fig. 1B). Ventrally, the glenoid part of the scapula continues into the coracoid, which curves medially (Osborn and Mook, 1921; Ikejiri, 2004). The dorsal part of the scapula is craniocaudally expanded, with a rugose vertebral margin, which indicates the presence of a cartilaginous suprascapula. The coracoid is rounded to oval in outline, with a rugose medial margin. The glenoid portion of the scapula is twice as long as that of the coracoid. The angle between both glenoid portions is acute (ca. 70°), so that the glenoid fossa is a rounded V-shaped notch. The bony sternal plates of *Camarasaurus* are subcircular in juveniles (Fig. 1A and

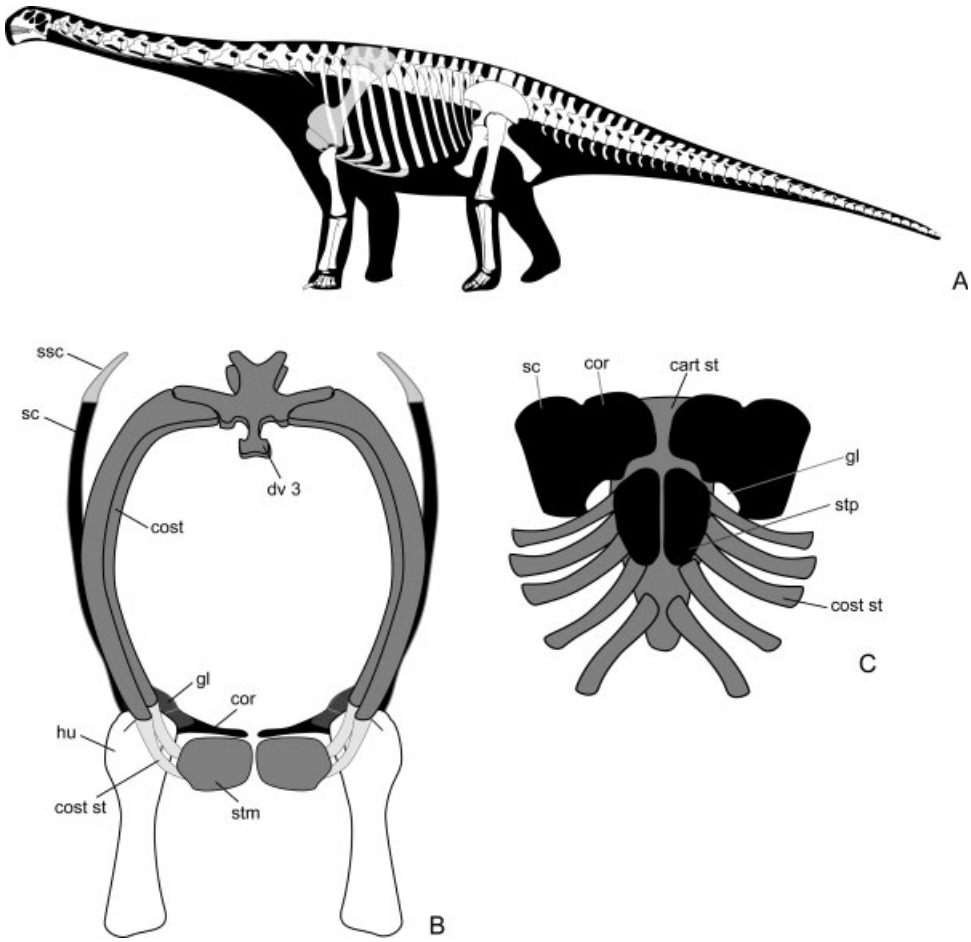

Fig. 5. Reconstruction of the pectoral girdle of *Camarasaurus* on the basis of the skeleton of *Camarasaurus lentus* (CM 11338). **A:** Reconstruction of the skeleton in left lateral view with an angulation of the scapula of 70° to the horizontal plane. **B:** Oblique caudal view of the shoulder girdle at the level of the second and third dorsal vertebra showing position of the glenoid and curvature of the scapulocoracoid. **C:** Ventral view of the sternal plates and their contact with the coracoids and sternal rib segments. Not to scale. cart st, sternal cartilage.

B) and become longitudinally oval in adults, where they are approximately as wide as the coracoids (Osborn and Mook, 1921; Gilmore, 1925; Ikejiri, 2004). Their medial margin can be straight or irregularly wavy and all margins of the sternal plates are broadened and rough.

The rugose medial margins of the coracoids indicate that the coracoids of *Camarasaurus* most probably contacted each other by cartilage in the median plane. The ontogenetically changing outline of the sternal plates would be consistent with their embedding in cartilage and subsequent enchondral ossification (Ikejiri, 2004). The bony sternal plates probably were connected by means of cartilage to the caudal margins of the coracoids and lay parallel to the caudoventrally descending line of the distal termini of the dorsal ribs (Fig. 5). Mobility between the sternal plates and the coracoids cannot be excluded. The width of the trunk increased between the first and probably the fourth dorsal vertebra, making the scapulae converge cranially. With a cranioventral inclination of the scapulocoracoid of approximately 60–65° to the horizontal plane in side view (Fig. 5A), a cartilaginous contact between the cranial margins of the bony sternal plates and the caudal margins of the coracoids would be possible. In this position, the scapula would have overlain the lateral surface of the first to fourth dorsal ribs. The dorsal margin of the scapula lay level with the neural arches of the vertebrae. If the suprascapula is reconstructed to have reached the level of the tips of the neural spines, it would have had one-third the height of the scapula. The coracoid then would be placed cranially to the rib cage (Fig. 5B and C).

The head of the humerus of *Camarasaurus* reaches two-thirds of the width of the glenoid (e.g., Osborn and Mook, 1921; Ikejiri, 2004). The medially curved coracoid would have resulted in a long axis of the glenoid fossa oriented from medioventrally to laterodorsally (Fig. 5B). The coracoidal part of the glenoid fossa would then lie craniomedially and ventrally with respect to the scapular part. As a consequence, the humerus of *Camarasaurus* would fit vertically into the glenoid fossa and the forelimb would support the trunk directly lateroventrally to the rib cage (Fig. 5B). Because there are no clavicles preserved in *Camarasaurus*, nothing can be said about a possible tilting of the scapulococoracoid or bracing of the shoulder girdle. However, the slightly more laterally positioned scapular glenoid portion would

have restricted protraction of the humerus in *Camarasaurus* more than in *Diplodocus*, resulting in a shorter stride length.

The angulation of the scapulocoracoid as reconstructed here for *Camarasaurus* resembles the reconstructions of Osborn and Mook (1921) and Jensen (1988), but differs strongly from that of Gilmore (1925). With a scapular inclination of 60–65° to the horizontal plane and a medially displaced coracoid, the shoulder girdle would have been situated more dorsal to the ilium than in previous reconstructions. Assuming straight columnar fore and hind limbs, the trunk of *Camarasaurus* would then decline in height from the pectoral to the pelvic girdle.

Opisthocoelicaudia. When articulated, the dorsal vertebrae of *Opisthocoelicaudia* formed an almost straight line. The second to fourth dorsal ribs show a distal expansion. The fifth through caudalmost dorsal ribs are long and slender, without a trace of a distal expansion (Borsuk-Bialynicka, 1977). In lateral view, the first to fifth dorsal ribs are curved ventrally, with their distalmost part bend caudally, and increase in length, thus making the line of their distal termini descend caudoventrally.

The scapula of *Opisthocoelicaudia* is dorsomedially curved, and the coracoid bends ventromedially (Borsuk-Bialynicka, 1977). The scapular blade is lightly expanded in longitudinal direction and rugose. Most likely, a suprascapula was present. The coracoid is nearly rectangular in outline and its medial margin is longitudinally expanded and rugose. The glenoid portions of scapula and coracoid are similarly long and form together a trough-shaped, medially widely open glenoid fossa with articular surfaces offset with respect to each other (Wilson and Sereno, 1998). The bony sternal plates are crescent-shaped in outline with a strongly concave lateral margin. Their medial margin is nearly straight, longitudinally expanded, and rugose. Two circular rugosities at the caudal margin of the bony sternal plates represent probably attachment areas for cartilaginous sternal rib segments (Borsuk-Bialynicka, 1977). The expanded distal ends of the cranial four dorsal ribs indicate the presence of such sternal rib segments (Fig. 6).

There are different alternatives for the arrangement of the sternal plates and coracoids in *Opisthocoelicaudia*. If the left and right coracoid of *Opisthocoelicaudia* would be arranged to contact each other along the midline, the resulting width would possibly be smaller than the width of the rib cage, although differences in the inference of rib orientation and articulation could change body wall width. In any case, the combined width of the left and right shoulder girdle would be much smaller than the width of the sacral region of *Opisthocoelicaudia*. The shoulder girdle of *Opisthocoelicaudia* is therefore mostly reconstructed with the coracoids being lateromedially widely separated from each other, probably medially connected by a broad shelf of cartilage (see Borsuk-Bialynicka, 1977: Fig. 4; Wilson, 2005b: Fig. 1.14). Assuming a wide median gap between left and right coracoid (Fig. 6B and C), and a position of the sternal plates caudally adjacent to the coracoids parallel to the distal termini of the dorsal ribs (Fig. 5C), the contact between the medial margin of the coracoids and the lateral margin of the sternal plates is possible, if the scapulocoracoid is inclined caudally at an angle of approximately 55–60° to the horizontal plane (Fig. 6A–C). The scapula then overlay the cranial four dorsal ribs and its dorsal margin ended level with the ventral face of the vertebral centra. The suprascapula would reach one-fourth of the height of the scapular blade (Fig. 6A). The coracoid would be placed laterally to the first and second dorsal rib (Fig. 6B), so that the humerus would lie laterally to the rib cage. In this reconstruction, the sternal rib elements would insert laterally at the cartilage embedding the sternal plates (Fig. 6C) due to the position of the coracoids and sternal plates, which contrasts the original reconstruction of Borsuk-Bialynicka (1977) with only the cranialmost two sternal ribs attached to the sternal plates. With a 55–60° caudal inclination of the scapulocoracoid in *Opisthocoelicaudia*, the shoulder girdle would have risen above the level of the ilium, so that the dorsal contour would have ventrally declined toward the sacrum (Fig. 6A).

The broadened and rugose medial margin of the coracoid is shorter than the concave part of the lateral margin of the bony sternal plates and both margins would fit into each other. As an alternative reconstruction, it is possible that the bony sternal plates of *Opisthocoelicaudia* were positioned medially adjacent to the coracoids, exceeding the length of the coracoid cranially and caudally, both being embedded in a cartilaginous frame (Fig. 6B and C). This reconstruction would coincide with the reconstructed width of the trunk at the first dorsal vertebra (although again, reconstruction of trunk width is dependent on the assumed rib articulation and might therefore change), and with the caudally descending line of the distal rib cage, and be consistent with the width of the sacral region in titanosaurs (Wilson and Carrano, 1999; Wilson, 2005a, 2005b). In this case, the contact between the medial margin of the coracoids and the lateral margin of the sternal plates would be possible if the scapulocoracoid was inclined caudally at an angle of approximately 60–65° to the horizontal plane (Fig. 6A–C). The scapula then would overlay the cranial three dorsal ribs and its dorsal margin ended level with the ventral face of the vertebral centra. If so, the suprascapula would have reached one-third of the height of the scapular blade (Fig. 6A). The coracoid then would be placed ventrolaterally to the first and second dorsal rib (Fig. 6B), so that the humerus would lie ventrolaterally to the rib cage.

A 55–65° caudal inclination of the scapulocoracoid in *Opisthocoelicaudia* results in a higher pectoral girdle with respect to the sacral region. The dorsal vertebrae then would have stronger ventrally declined toward the sacrum (Fig. 6A). The reconstructed orientation of the scapulocoracoid of 55–60° or 60–65° to the horizontal plane suggests that the coracoidal part of the glenoid faced lateroventrally and was positioned caudoventrally to the scapular part. The scapular part of the glenoid then would face caudomedially (Fig. 6B). The head of the humerus of *Opisthocoelicaudia* is about half as wide as the glenoid fossa and with this orientation of the glenoid could be inserted at the proposed slightly laterally abducted angle (Wilson and Carrano, 1999; Wilson, 2005b). The orientation of the glenoid fossa possibly allowed a larger retraction as well as ad- and abduction of the humerus compared to other sauropods, therefore a larger forelimb mobility and stride length (Carrano, 2005).

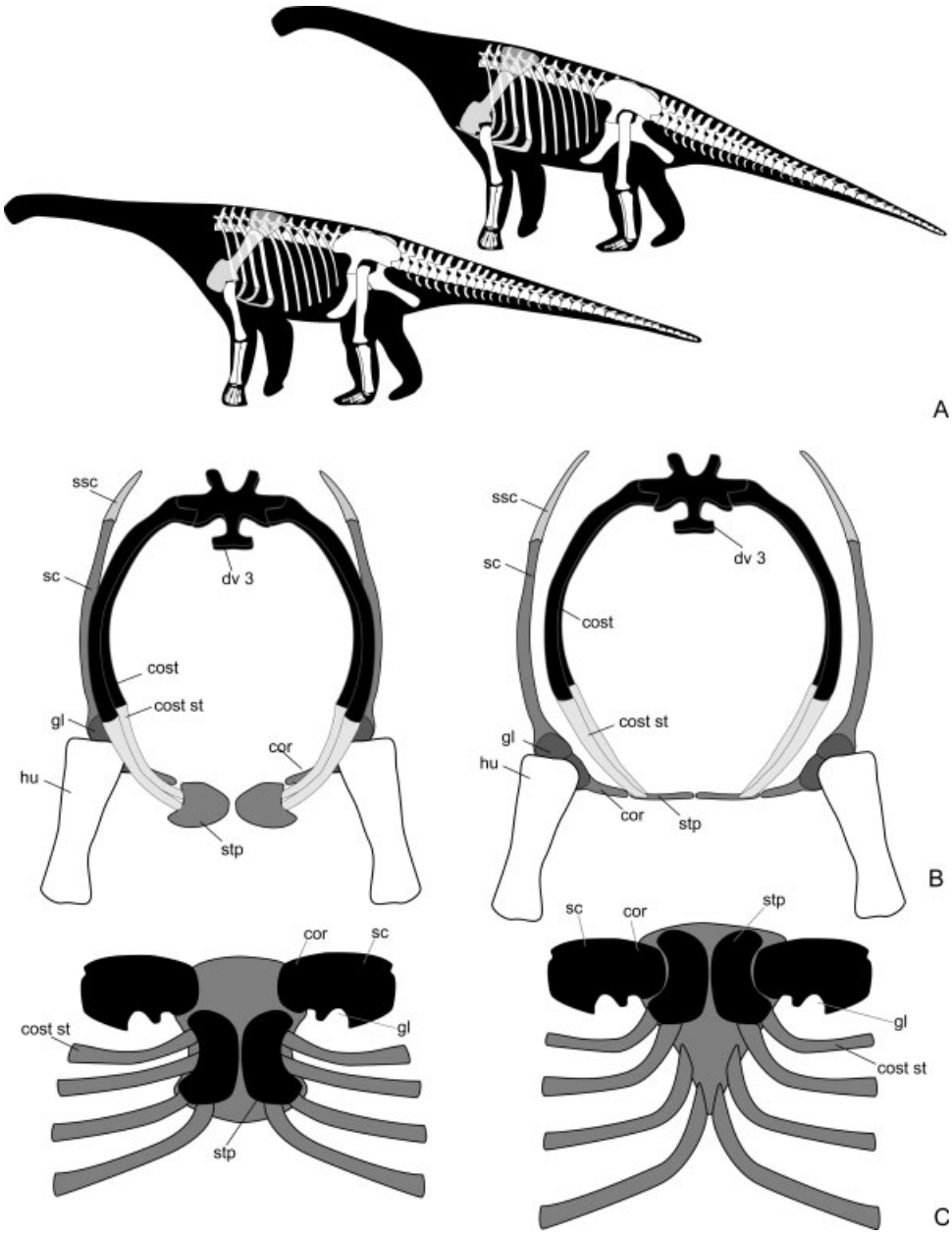

Fig. 6. Reconstruction of the pectoral girdle of *Opisthocoelicaudia* on the base of the skeleton of *Opisthocoelicaudia skarzynskii* (ZPAL MgD-I/48) as published in Borsuk-Bialynicka (1977); neck and skull are unknown. Two alternative reconstructions are possible concerning the relationship between the coracoids and sternal plates: left side displays reconstruction with the sternal plates lying caudally adjacent to the coracoids; right side is reconstruction with the sternal plates positioned between the coracoids. **A:** Reconstruction of the skeleton in left lateral view, left side with angulation of the scapulocoracoid of 55° to the horizontal plane (corresponding to sternal plates positioned caudally to the coracoids), right side with angulation of the scapulocoracoid of 65° to the horizontal plane (corresponding to sternal plates positioned between the coracoids) leading to a higher pectoral girdle with respect to the sacrum. **B:** Oblique caudal view of the shoulder girdle at the level of the second and third dorsal vertebra showing position of the glenoid and curvature of the scapulocoracoid. **C:** Ventral view of the sternal plates and their contact with the coracoids and sternal rib elements. Not to scale.

There is no osteological evidence for bony sternal plates angled against each other and having a mutual contact only at their cranial termination, as was suggested by Borsuk-Bialynicka (1977: Fig. 5). Because of their distal dilatation, it appears highly unlikely that the cranial two ribs did not have any cartilaginous extensions (Borsuk-Bialynicka, 1977). The reconstructed overall configuration of the pectoral girdle in *Opisthocoelicaudia* differs from other reconstructions (e.g., Borsuk-Bialynicka, 1977; McIntosh et al., 1997; Wilson and Sereno, 1998) mostly in the inclination of the scapulocoracoid, and, if the sternal plates are positioned be-

tween the coracoids, also in the relationship between coracoids, sternal plates, and sternal ribs.

DISCUSSION

Humerus Articulation

In many previous reconstructions, the transverse curvature of the scapulocoracoid was completely ignored and the shoulder girdle was treated as a two-dimensional structure in lateral aspect. The vertical orientation of the humerus does not only hinge on a ventrally open glenoid fossa, but also on its morphology, the curvature of the scapulocoracoid, and the shape of the cranial part of the rib cage. If the glenoid is mediolaterally directed and not a longitudinally oriented trough, the humerus can still be held vertical, even if the cranioventral inclination of the scapulocoracoid is more than 50° (see also Bonnan, 2003: Fig. 6B).

The head of the sauropod humerus is sculptured with grooves and bulges (Fig. 1B and C), which indicates the presence of a cartilaginous articular cap of unknown dimensions (Christiansen, 1997; Carter et al., 1998; Paul and Christiansen, 2000; Holliday et al., 2001; Bonnan, 2003, 2004). In this context, the presence of a distal articular cartilage capsule in a sauropod humerus (*Cetiosauriscus*, Kimmeridgian of Switzerland) is interesting, because it shows the general presence of articular cartilage in sauropods (Schwarz et al., 2007). In most fossils, the size of the bony glenoid fossa exceeds that of the preserved osseous head of the humerus and there is no exact match of the shoulder joint. This makes a reconstruction of the mobility of the humerus, especially of the excursion angle of pro- and retraction, difficult, although functional morphological considerations make it possible to constrain the relationships of the limb bones to each other (Bonnan, 2003, 2004). The excursion angle for the humerus protraction depends also on the orientation of the glenoid fossa and the possibility of a rotation of the scapulocoracoid along clavicular and/or coracosternal joints (see reconstruction of *Diplodocus* above and conclusions below). Furthermore, protraction of the humerus could have been combined with its abduction and craniolateral rotation around its long axis in the terminal protraction phase.

Muscular stabilization of the shoulder joint was required during locomotion, e.g., by means of m. coracobrachialis brevis, m. dorsalis scapulae, m. scapulohumeralis posterior, and m. subcoracoscapularis (Jenkins and Goslow, 1983; Bonnan, 2004). Furthermore, a possible restriction of the movements of the scapulocoracoid in sauropods would enhance better stabilization of the glenoid.

Orientation of Scapulocoracoid and Suspension of Vertebral Column

In quadruped tetrapods, the cranial part of the thorax and the base of the neck are suspended in a muscular sling, in which the m. serratus complex plays a dominant role (Frey, 1988b; Kardong, 1998; McGowan, 1999; Salisbury, 2001). For sauropods, a similar sling suspension in the shoulder region must have existed in order to intercept the forces caused by the body mass when the forelimbs are set. Reconstructions of the major muscle groups that support or move the scapulocoracoid are required, for which extant Crocodylia and Aves can serve as models.

The scapula of sauropods resembles with its concave cranial and caudal margin and its cartilaginous suprascapular seam that of extant crocodylians (Figs. 1 and 2). The same holds true for the shape of the cervical ribs of sauropods with their longitudinally oriented bodies. In such a crocodylian model, M. serratus profundus would have originated from the medial surface of the dorsal part of the scapular blade, and inserted on the rugose dorsal margins of the posterior cervical ribs such as in extant crocodylians (Fig. 7A). M. serratus superficialis would likewise have originated caudally from the medial surface of the suprascapula and the caudal margin of the scapula, its cranial fiber bundles pulling ventrally, the caudal ones caudoventrally, and inserted on the rugose craniolateral crests of the cranial four to six pairs of dorsal ribs. M. rhomboideus would have originated from the medial surface of the suprascapula and the dorsal half of the scapular blade (Fig. 7A), pulled craniodorsally, and merged with the lateral fibers of the dorsalmost epaxial muscles at the cervicothoracic junction (Frey, 1988a). M. levator scapulae would have originated on the lateral and medial surface of the concave cranial margin of the scapular blade (Fig. 7A), extending from there over the entire length of the neck to insert on the lateral rugosity of the cranial processes of the cervical ribs (Frey, 1988a). The long scapular blade provided attachment area for m. teres major as in extant crocodylians, which could have merged with fibers from m. dorsohumeralis (Fig. 7A). M. dorsohumeralis probably was attached to the lumbodorsal fascia and the dermis as in *Alligator*. If so, the muscle provided mechanical coherence between shoulder girdle, body wall musculature, and the dermis. M. costocoracoideus (= m. sternocoracoideus in birds) would have been divided into a superficial and profound part (Fürbringer, 1876; Meers, 2003). Its pars superficialis would have originated from the lateral surface of the cranialmost sternal ribs and the sternal plates, and inserted at the caudal margin of the coracoid ventrally to the coracoidal glenoid (Fig. 7B). M. costocoracoideus profundus would have inserted caudally to the pars superficialis at the distal termini of the dorsal ribs and from there would have extended cranioventrally to insert at the medial surface of the coracoid (Fig. 7B) (Brinkmann, 2000; Meers, 2003). An insertion of this muscle at the last cervical ribs, as described for modern crocodylians, is due to the large distance between this cervical rib and the coracoid unlikely in sauropods (Fürbringer, 1876; Brinkmann, 2000).

The possibly close contact of the scapula with the dorsal ribs as indicated by the presence of rib facets in sauropods (Bonnan et al., 2005) and the presence of clavicular bones are similar to extant birds, which would also allow a more bird-like reconstruction of these major muscle groups. In such an avian model, m. levator scapulae would be absent (Fisher and Goodman, 1955; George and Berger, 1966; Zusi and Bentz, 1984; Vanden Berge and Zweers, 1993). M. serratus profundus would have originated from the dorsal third of the medial surface of the scapular blade, and inserted laterally on the proximal parts of the cranialmost dorsal ribs and on the rugose dorsal margins of the caudalmost cervical ribs (Fig. 7E). M. serratus superficialis would be divided into a pars cranialis and a pars caudalis. M. serratus superficialis pars cranialis would attach to the ventral part of

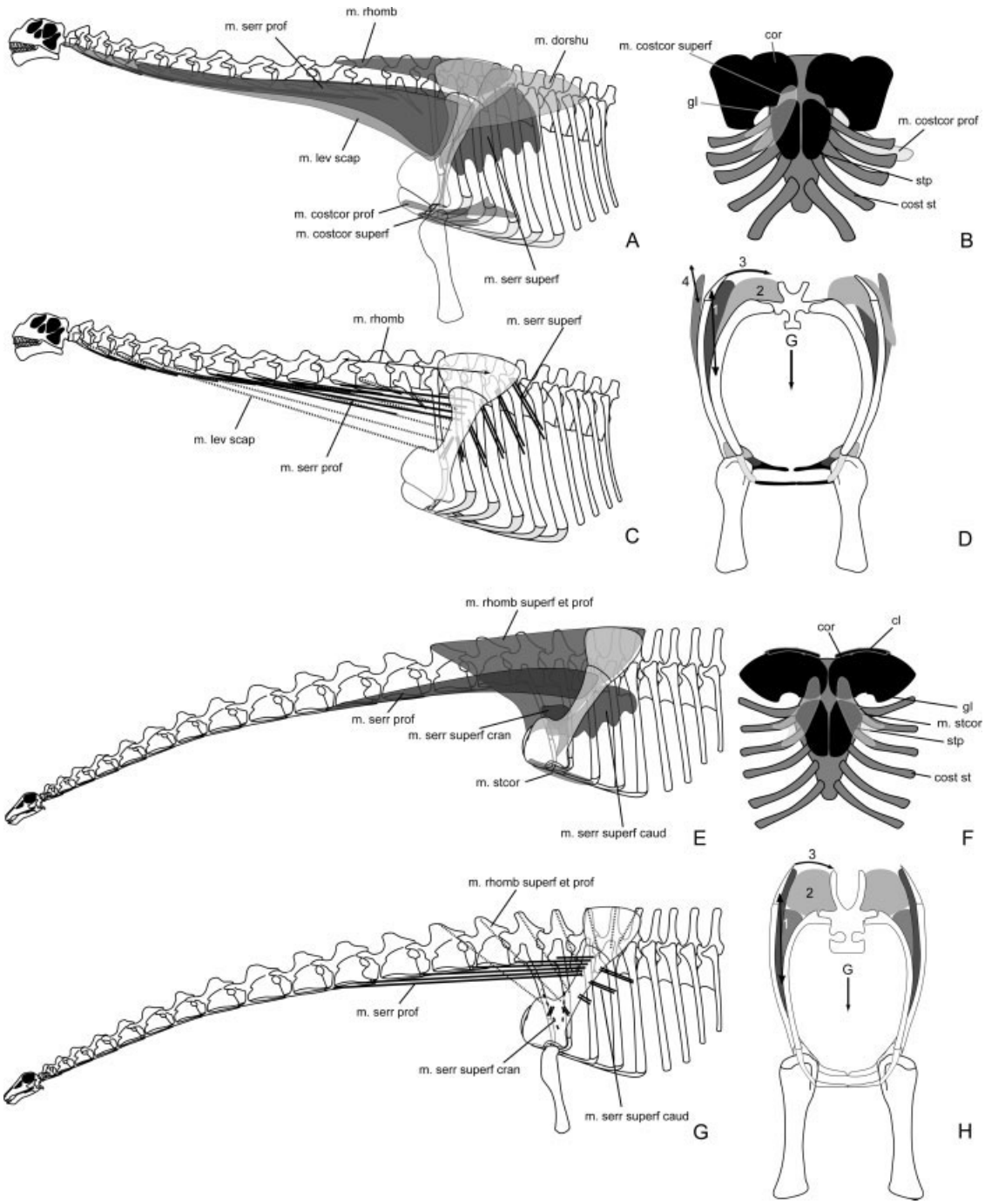

Fig. 7. Reconstruction of the main muscles of scapulocoracoid and suspension of the trunk in sauropods. *Camarasaurus* neck and pectoral girdle in left lateral view with the crocodylian model of muscles around the scapulocoracoid. **A:** Reconstruction of main muscles of scapulocoracoid. **B:** Ventral view of pectoral girdle with reconstructed distribution of m. costocoracoideus. **C:** Suspension of the trunk from the shoulder girdle by means of the m. serratus complex, connection between suprascapula and epaxial neck musculature by m. rhomboideus, left lateral view. **D:** Cross-section of the pectoral region at the level of the second dorsal vertebra showing suspension of the shoulder girdle. The body is loaded by gravity (G), the m. serratus complex suspends axial skeleton from the scapula (1), scapula and suprascapula are hydraulically stabilized by the underlying epaxial musculature (2) against medial bending (3), and additional position control of the shoulder girdle is provided by the connection between scapula and dermis by means of m. dorsohumeralis (4). *Diplodocus* neck and pectoral girdle with the avian model of pectoral muscles. **E:** Reconstruction of main muscles of scapulocoracoid in left lateral view. **F:** Ventral view of pectoral girdle with reconstructed distribution of m. sternocoracoideus. **G:** Suspension of the axial skeleton from the shoulder girdle by means of the m. serratus complex, left lateral view. **H:** Cross-section of the pectoral region at the level of the second dorsal vertebra showing suspension of the shoulder girdle. The body is loaded by gravity (G), the m. serratus complex suspends the scapula from the axial skeleton (1), and scapula and suprascapula are hydraulically stabilized by the underlying epaxial musculature (2) against medial bending (3). Not to scale. m. costcor prof, m. costocoracoideus profundus; m. costcor superf, m. costocoracoideus superficialis; m. lev scap, m. levator scapulae; m. rhomb, m. rhomboideus; m. rhomb superf et prof, m. rhomboideus superficialis et profundus; m. serr prof, m. serratus profundus; m. serr superf, m. serratus superficialis; m. serr superf cran, m. serratus superficialis cranialis; m. serr superf caud, m. serratus superficialis caudalis; m. stcor, m. sternocoracoideus.

the medial surface of the scapula, dorsally to the scapular glenoid, and from there extend to the ventral half of the cranialmost two or three dorsal ribs (Fig. 7E). M. serratus superficialis pars caudalis would have had a nearly similar distribution as in the crocodylian model, but its insertion would have been restricted to the scapular blade. As the scapular blade in sauropods covers much of the lateral face of the cranialmost dorsal ribs, it is unlikely that m. serratus superficialis could have contained another subdivision, m. metapatagialis, which connects in birds the cranial dorsal ribs with the skin (George and Berger, 1966; Vanden Berge and Zweers, 1993). The largest muscle of the scapula would have been m. rhomboideus superficialis et profundus (Fisher and Goodman, 1955; George and Berger, 1966), originating from the craniomedial surface of the scapular blade and acromion, and possibly the medial surface of the suprascapula (Fig. 7E). M. rhomboideus would have inserted at the apices of the neural spines of the caudalmost cervical and the cranial dorsal vertebrae. If m. rhomboideus in sauropods occupied as much space at the medial scapula as in modern birds, it is likely that it inserted also at the distal margins of the claviculae (Fig. 7E). M. sternocoracoideus would have extended from the external surface of the sternal plates and cranialmost sternal ribs cranially to insert at the external surface of the coracoid ventrally to the coracoidal glenoid (Fig. 7E and F) (George and Berger, 1966; Zusi and Bentz, 1984; Baumel et al., 1993).

The lack of distinct insertion areas for these major muscles at the scapula of sauropods makes it difficult to judge about the configuration of the reconstructed scapulocoracoidal musculature in favor of one or the other hypothesis. According to the assumption that similarly shaped bones indicate a similar load implied by muscle activity during locomotion (see Materials and Methods above), the structural similarities in the osteology of the shoulder and neck base area would allow the reconstruction of the major muscle groups based on the myology of extant crocodylians. On the other hand, the overall configuration of the sauropod pectoral girdle with bony sternal elements, claviculae, and a possibly closer contact between scapulocoracoid and dorsal ribs is more birdlike, which equally justifies reconstruction of the shoulder myology based on extant birds.

Under the assumption that the scapulocoracoid in sauropods was inclined cranioventrally with 60° or more to the horizontal plane as reconstructed in the examples here, with the crocodylian model of sauropod pectoral muscles, m. serratus profundus and superficialis would have formed a muscular sling that suspended the trunk on the supporting extremity, as reported in other amniotes (Fig. 7C and D). The load of trunk weight is transferred from the shoulder girdle to the cranial region of the thorax. M. rhomboideus would have connected scapula and suprascapula with the epaxial neck musculature (Fig. 7C), whereby the underlying epaxial musculature hydraulically stabilized the flexible suprascapula against medial bending under load by the body mass, as it has been described for extant Crocodylia (Fig. 7D) (Frey, 1988b; Salisbury and Frey, 2001). During the swing phase of the limbs, additional position control of the shoulder girdle would have been guaranteed by the connection between scapula and m. dorsohumeralis (Fig. 7D).

With the avian model of sauropod pectoral muscles, again the m. serratus complex would have been a most significant part of this muscular sling (Fig. 7G and H). The size and dorsal pull of m. rhomboideus would require a large antagonistic muscle, a counterpart that could have been taken over by m. serratus superficialis pars caudalis (Fig. 7G and H). In the case of locomotion, loads acting on the swinging forelimbs would have been translated by m. rhomboideus to the neural spines in the base of the neck. The loaded neck base would therefore have needed to be stabilized effectively by strongly segmented, large epaxial muscles. As in the crocodylian model, the underlying epaxial musculature would have hydraulically stabilized the flexible suprascapula against medial bending under load by the body mass (Fig. 7H).

CONCLUSIONS

The classic reconstruction of the pectoral girdle of sauropods with an angle of less than 45° to the horizontal plane has been based on insufficient fossil data and a reductionistic view of the osteological evidence. The result was a pectoral girdle, which was anatomically unlikely especially concerning the subvertical orientation of the coracoids in front of the cranial thoracic aperture, not known in extant quadrupeds. Combining phylogenetic and comparative morphological suites yields now a reconstruction of the shoulder girdle, which is consistent also with reconstructions of the pectoral musculature and functional morphological demands.

If the reconstruction of the pectoral girdle of sauropods is based on that of extant Crocodylia, the shoulder muscles can be reconstructed without any contradiction to osteology and are fully coherent with the demands of a muscular sling supporting the cranial part of the axial skeleton. The reconstructed muscular sling would correspond to the classical adaptable suspension of the shoulder girdle by means of the m. serratus complex as in other tetrapods (Kardong, 1998; McGowan, 1999). An effective muscular sling by m. serratus can also be reconstructed if a more avian-like model of the shoulder girdle musculature is applied. This muscular sling would require effective stabilization of the neck base. However, as both models yield an effective muscular suspension of the shoulder girdle at the vertebral column, none can be preferred against the other.

Reconstructions of scapulocoracoid mobility (i.e., tilting or rotation of the scapula and translation of the coracoids) depends on the presence and arrangement of claviculae, the presence of a coracosternal joint, and on the reconstruction of appropriate muscles for moving the scapula and coracoid. In the crocodylian model, cranial rotation of the scapula of sauropods could have been achieved at least by means of m. levator scapulae (Fig. 7A and C), whereas m. costocoracoideus (Fig. 7B) and other muscles could have pulled the coracoid caudally relative to the sternum, as in modern crocodylians (Meers, 2003). Movements of the scapulocoracoid would require a mobile intercoracoidal or coracosternal articulation. If so, then combined cranial scapular rotation and coracoid movement would help to increase stride length in the forelimbs of sauropods, possibly supported by a non bracing arrangement of the claviculae.

In contrast, the avian model of the shoulder musculature would indicate a closer connection of the scapula to

the dorsal ribs. Muscles contributing to the movement of the scapula would be much smaller (m. serratus superficialis pars cranialis et caudalis) or completely absent (m. levator scapulae, m. metapatagialis), thus indicating much more restricted movements of the scapulocoracoid. M. sternocoracoideus (Fig. 7F) could as in other archosaurians (Bonnan et al., 2005) achieve a caudal movement of the coracoid, but only in the case of the assumption of a mobile coracosternal joint. This model would therefore indicate more restricted movements of the scapulocoracoid in sauropods (possibly combined with an overlapping arrangement of the claviculae), combined with a possibly stronger stabilization of the glenoid.

Possibly, some sauropods, such as *Opisthocoelicaudia*, combined the retraction movements with abduction and rotation, implying hypothetically large degrees of liberty for the mobility of the humerus. Possibly, the assumed glenoid cartilage in the humeroglenoidal joint (no matter if present only as thin layer or as a thick pad) could act as shock absorber additional to the muscular pectoral sling. Two alternatives can be offered for the arrangement of the sternal plates in reference to the coracoids. However, both of these models are consistent with the width of the sacral region in titanosaurs.

The differences in configuration of the pectoral girdle in different sauropods as reconstructed here have also important effects for the overall body posture, as they indicate differences in the dorsal contour between different sauropods and therefore different trunk construction types.

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